Insects in the population dynamics of plants

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There are three possible influences that insects can have on the abundance of a plant: they can increase it, have no effect, or decrease it. For the purpose of this discussion, I have assumed that a change in the vigour of a plant or its seed production results in a similar change in its abundance. However, it is possible, because of over-compensation, that the long-term result is in the opposite direction to that of the short-term one. In other words, an increase in seed production may lead to a lower overall density of the plant.

Increase in the abundance of a plant species as a result of insect activities

Activity essential for the survival of some plant species

One insect activity that is essential for the survival of many plant species is pollination. Insects can cross-pollinate plants with smaller amounts of pollen and at a lower density than can be achieved by wind. This ability is at a premium in tropical rain forests which are typified by a large number of plant species each at a low density. Additional factors that militate against wind pollination are lack of a leafless period, frequent rainfall, dense forest structure (as it reduces wind velocity) and lack of unambiguous stimuli to co-ordinate flowering (Whitehead 1969). Under these conditions, all typical of the wet tropics, many highly specialized pollinators have evolved. Yeo* (1972) has mentioned the Euglossini bees. According to Janzen (1971) they may fly over 24 km from nest to foraging area and at least 3·6 km to obtain a pollen load. Six trips like this may be made to complete a regular daily round of plants. Pollinators are of course also essential for the survival of many plants in northern latitudes. One of the classic examples mentioned in most textbooks of entomology is *Yucca flamentosa* Fern which is dependent on the moth *Tegeticula yuccasella* Riley for pollination. Although *Yucca* can survive over a wide climatic zone, its natural distribution is restricted to that of this moth whose larvae feed on *Yucca* seeds (Riley 1892).

* References in small capital letters refer to other papers in this volume

Stimulation of plant growth and reproduction as a result of insect attack

There are other types of insect activity that are not essential for the survival of the plant species, but they increase vegetative growth and reproduction. It is a fallacy that consumption of leaves, buds, flowers and other plant tissue by insects necessarily reduces plant vigour or reproductive capacity. On the contrary, both vegetative growth and reproduction may be increased. For example, even with major pest species, such as the cotton bollworm *Heliothis obsoleta* F., the situation is not simple: one bollworm may destroy up to three bolls, a figure that approaches a quarter of the production of a single plant. However, Tanskiy (1969) showed that the removal of three bolls per plant during the first larval generation of the bollworm increased the yield of bolls by 23·8 per cent. It was only during the second and third larval generations that this level of loss reduced the yield. The effects of this pest have been imitated as a means of increasing cotton yields. Eaton (1931) found that manual destruction of cotton flowers before 25th July increased fibre yields by 33 per cent and the weight of seed by 43 per cent when all flowers but one per branch were removed. But even with complete destruction of early flowers, yield was higher than in the controls. I suspect that this applies to many plants besides cotton and that often the control of low populations of so-called pest insects may produce lower yields.

Much the same story applies to defoliation if it is done at the correct time. Mueggler (1967) found that defoliation of *Potentilla gracilis* Dougl. by clipping, shortly after leaf growth began in the spring, stimulated both herbage and flower stalk production. Skuhravý (1968) reported that in Czechoslovakia 50 per cent defoliation of late potatoes between the second week in June and the end of July increased tuber yield in September from 13·2 to 26·2 per cent. Even complete defoliation was not necessarily detrimental. Similarly, Ellison (1960) found that light browsing (65–70 per cent of the current year's growth) on several species of shrubs had invigorating effects, but that these wore off unless the stimulus was repeated annually.

A partial annual defoliation by insects is usual for most species of perennial plants. On the basis of clipping experiments, it appears that moderate levels of defoliation, possibly with up to half the leaves removed, are likely to be stimulatory when carbohydrate reserves of the plant are high and there is time before winter for the plant to recover. In most herbaceous perennials, this is after the first flush of spring growth but before bud formation (Jameson 1963). A similar defoliation at other times is likely to be damaging. For example, Maun & Cavers (1971*a*) found that the cauline leaves removed from curled dock (*Rumex crispus* L.) during flowering reduced mean seed size by about a third. Neither seed number nor viability was affected, but it has been established for many plants that seedlings from small seed have a higher mortality than those from larger seeds (Black 1958; Kaufmann & McFadden 1963). Hence, this defoliation would tend to decrease the size of the subsequent generation of dock.

The maturity of the leaf attacked by insects also has a bearing on whether the plant is stimulated. Contrary to conventional wisdom, insect attack on young leaves of a deciduous plant is more stimulating to the plant than attack on mature leaves. Young leaves are in fact an energy drain to the plant while damage to mature leaves represents a loss in the photosynthetic capacity of the plant. However, the stimulating effect of the removal of young leaves is not so much the elimination of this drain, but an increase in the photosynthetic rate in the mature leaves. The findings of Maggs (1964) and Sweet & Wareing (1966) suggest that the photosynthetic rates in plant leaves are normally well below the maxima of which they are capable. The vegetative growth of a plant, and its reproductive

capacity, can be greatly increased if the assimilation rate can be increased without a corresponding production of photosynthetic area. These effects are reflected by the work of Taylor & Bardner (1968) with *Plutella maculipennis* (Curt.) and *Phaedon cochleariae* (F.) on turnip. The latter species, which feeds preferentially on mature leaves, produced a slight increase in root yield over the control when there were only five larvae per plant, but with each additional larva there was a loss of 2·6 per cent in yield. In contrast, *Plutella* feeds indiscriminately on leaves of all ages and in all but one of the groups of attacked plants, yield was more than in the unattacked controls. I suggest that the result would have been still more striking if *Plutella* had fed preferentially on immature leaves. Many leaf-feeding insects do in fact feed almost exclusively or preferentially on young foliage, and attack by such insects may often be stimulating, rather than damaging to the plant. Indeed, properly managed, the potato beetle might conceivably be used to increase potato yields in Britain.

Increase in vegetative reproduction as a result of insect attack

Many aquatic plants are readily propagated from pieces of stem. An insect whose attack results in sectioning of the stem is likely to increase and spread the weed. There do not appear to be any recorded examples of this, but it is indeed one of the fears of people undertaking the biological control of aquatic plants.

Increase in seed size and hence seedling survival as a result of insect attack

A decrease in the number of seeds produced by a plant, as a result of an insect attack on the flowers or immature fruit, should increase the size of those seeds which escape damage. For example, Maun & Cavers (1971*b*) found that for curled dock (*R. crispus*) there was a progressive increase in both seed size and the thickness of the seed coat as an increasing proportion of flowers was removed: mean weight per seed when 75 per cent of the flowers were removed was 1·87 mg compared with 1·42 for the controls. This process is essentially the same as thinning apples to get a few large fruit rather than many small ones. The importance of this to the population dynamics of the plant is that, as already mentioned above, there is a higher survival of seedlings from large seeds than from small ones and they make larger, more productive plants (Black 1958; Kaufmann & McFadden 1963). Hence, particularly under highly competitive or severe conditions, an insect attack on the flowers may have the effect of increasing the survival of a plant species. The effect of the increased thickness of the seed coat, noted by Maun & Cavers (1971*a*), was to delay germination. If germination were staggered over a long period its effect could be to damp population fluctuations from other causes; but delayed germination could be either beneficial or detrimental to the plant species depending on the conditions.

No effect on the abundance of a plant species as a result of insect attack

I suspect that most insect species, most of the time, have little effect on plant abundance. However, in the context of this volume, this is less worth elaborating than either of the extremes. This aspect will therefore be discussed rather briefly; a few examples should

suffice. First, the cotton bollworm may destroy up to 14 buds per plant. However, 70–80 per cent of the buds produced by a cotton plant are normally shed without producing bolls in the absence of any infestation. This allows the plant to compensate for the bollworm by shedding a smaller percentage of the buds unless almost all the buds are destroyed (Tanskiy 1969). Secondly, there is the point that many insects which we regard as pests are not necessarily so from the plant's point of view. That a caterpillar makes a few holes in a cabbage does not necessarily harm the ability of the cabbage to perpetuate itself. Indeed, many of our so-called pest insect species are ones that produce 'cosmetic' defects in the crop that merely lower or destroy its sale value but which, from the point of view of the population dynamics of the plant, may be of little consequence.

Decrease in the abundance of a plant species as a result of insect activity

It is obvious that chewing insects make holes in plants, but it is not as easy as many people imagine to show that even such striking damage decreases the abundance of a plant. Indeed, most plant ecology books include sections on how soil and climate and plant competition influence plant abundance but make no mention at all of insects. Apparently plant ecologists believe that insects have only a superficial effect on the abundance of plant species. There are, however, several pieces of evidence that suggest insects can have a large effect.

Circumstantial evidence is afforded by the tendency of plants that are comparatively scattered in their native region to produce large dense stands when introduced into other parts of the world with few or none of their specialized insect enemies. The following examples are from Canada but surely similar examples could be found in many other parts of the world.

The first example is cypress spurge, *Euphorbia cyparissias* L. One of its many introductions was from Scotland to Braeside, Ontario, in 1870. The infestation was scattered over nine square miles in 1955, with spurge comprising about a third on a dry weight basis of the herbaceous vegetation. By 1970, the overall size of the infested area had increased to nearly 30 square miles. In Canada this weed has a rust that alternates on clovers, but no specialized insect enemies, whereas in Europe it has a complex of about 20 species. Leafy spurge, *Euphorbia esula* L. presents a similar problem. It was first noticed in 1920, and by 1940 had spread to infest between 35,000 and 45,000 acres, mostly on the Canadian Prairies (Harris & Alex 1971). Leafy spurge is not regarded as a serious weed in eastern Europe, the climatic analogue of the Canadian Prairies.

A survey of toadflax, *Linaria vulgaris* Mill., over approximately a third of the settled part of Saskatchewan showed that 134,000 acres were infested and that one stand, originally an acre in extent, expanded to 85 acres in five years. There were no insects specialized on toadflax present in Saskatchewan at this time, and an average of nearly 6000 seeds were produced per flowering stem (Harris 1961; Harris & Carder 1971).

To me, at this time, the most alarming problem in Canada is diffuse knapweed, *Centaurea diffusa* Lam. This weed was first collected in British Columbia in the early 1930s. At the present time it is estimated to cover a million acres in the Kamloops–Okanagan region of British Columbia, as well as being well established in the western central Kootenays. It is now beginning to spread into the east Kootenays, and threatens to occupy the whole dry belt of the province. There are many farmers and ranchers in this

area who cannot remember knapweed plants 20 years ago; now the weed has practically taken over the range, especially where heavy grazing has been practised. We have found no specialized insects on this weed in Canada but have turned up several in the Near East and in eastern Europe.

These examples are circumstantial because there are undoubtedly many other ecological changes involved besides the absence of insect enemies in the new environment.

Less circumstantial evidence is available following the accidental introduction of an insect to a new environment. The spruce sawfly, *Diprion hercyniae* (Htg.), is a dramatic example of what can happen when a European insect is introduced to Canada. In 1930, it was found defoliating over 2000 square miles in the Gaspé region. In the next few years, the sawfly spread throughout New Brunswick and southern Quebec. In the infested area, mortality of spruce was high, about 73 per cent for white spruce and about 45 per cent for black spruce. Fortunately for the Canadian forest industry, much of which is dependent on spruce, biological control by a virus together with insect parasites provided a very dramatic solution to the problem, but not before the insect had demonstrated how effective it could be in reducing the density of spruce in eastern Canada (McGugan & Coppel 1962).

The introduced insect currently best known to the people in Ontario is the elm bark beetle, *Scolytus multistriatus* (Marsh.), which is largely responsible for spreading Dutch elm disease. The effects of the beetle and the disease in Ontario are more devastating than they have been in Britain. The final outcome remains to be seen, but, at best there will be a great reduction of elms; possibly only widely scattered trees will remain.

The best information on the effects of insects on the population dynamics of plants can be obtained from 'case histories' concerning the biological control of weeds. This is because ideally, following the introduction of a new insect, both the population of the insect and that of the weed are closely monitored. The classic example is, of course, the control of the cactus, *Opuntia* spp., in Australia—a story which has been quoted many times. In 1925, *Opuntia* spp. infested 60 million acres; about half this area was so densely infested that the land was useless. A moth, *Cactoblastis cactorum* (Berg), was released in 1926 and within 4 years had destroyed the two main species of *Opuntia* over large areas. It has since restricted them to isolated plants and scattered clumps (Wilson 1960). If one recalls that the previously discussed weeds, spurge and toadflax, tend to be scattered where they are indigenous, but form large dense stands where they have been introduced without their enemies, it would appear that in Australia it has been possible to produce the indigenous type distribution pattern by introducing an insect parasite of the plant.

Another example is St John's wort, *Hypericum perforatum* L. This weed formed large dense stands on the west coast of North America, occupying over two million acres of range land in California alone. Several insects were introduced, one of them (the beetle *Chrysolina quadrigemina* (Suffr.)) was an almost instant success, practically eliminating the weed from open areas. St John's wort is a sun-loving plant, although it is slightly more shade tolerant than the beetle. The result is that today it is largely found in semi-shaded places in California. Huffaker (1957) suggested that an ecologist looking at the plant in California today, without knowing of its history, would conclude that the plant is shade loving and that, because the beetle is no longer prevalent, it has little effect on the weed.

The occurrence of small but dense patches of St John's wort in British Columbia in the 1940s caused concern in view of its ability to dominate range land in the western United States. In the early 1950s, the same five species of insect that had been tried in California were released in British Columbia. Three of the species died out but two, *C. quadrigemina*

and *C. hyperici* (Först.), remained at low densities for several years without affecting the weed. Eventually, after 6 to 13 years, various colonies of the beetles increased and reduced the St John's wort to about 2 per cent of its former density. Also, as in California, the weed has tended to retreat into the shade with the main concentration of the beetles at the edge of the shade. This seems to be a stable situation. However, unlike the Californian situation, two species of beetle were effective but in different habitats, with *C. hyperici* thriving in a moister region than *C. quadrigemina.* Neither species was effective in the semi-arid regions and we are still trying to find an insect for these places. The conclusion I want to draw from this is that different insects may be responsible for controlling the density of a plant in different parts of its ecological range.

I would like to discuss one more example of biological control of weeds. There are currently at least five studies in the world on the interaction between the cinnabar moth (*Tyria jacobaeae* L.) and the ragwort plant (*Senecio jacobaea* L.), and no two of them are producing identical results. I am involved with two of these projects and am getting different results on the east and west coasts of Canada. In both instances, establishment of the moth followed the same pattern. The moth at first catastrophically declined, followed by population maintenance for 2 years and then a four- to five-fold annual increase. As a result of this increase, on both the east and west coasts, the weed was completely defoliated. There the similarity ends. In the east the weed is being reduced to a very low density and in the west the number of plants has stayed almost the same. The reason for this difference seems to be an interaction with climate. On the west coast, the weed is defoliated by mid-June, but has regenerated by late September, sometimes to flower and produce seed, and sometimes as a rosette. The winters are mild, occasionally there is no frost at all, so the rosettes can build up their energy reserves over winter and with spring produce a new flower stalk. The main difference is that the average dry weight of flowering plants in the release field is approximately half of that of unattacked plants. In Nova Scotia, however, spring comes later so that the plants are not defoliated until late July. There is no regeneration before the relatively hard and early winter and no possibility of regeneration during winter. By spring the plants are dead. The eventual outcome of this remains to be seen; it may be that in Nova Scotia the insect will exterminate the weed locally and then itself die out, allowing the weed to return. Thus, the effect of the insect may be to produce fluctuations in the population of the weed. In contrast, in British Columbia it appears that the weed will be stabilized at a low density. This is the hoped-for result of biological control.

I suggest that the main effect of phytophagous insects on plants is to produce communities of many plant species, each at a low density and, other things being equal, each plant species will be rather regularly spaced. Janzen (1970) has discussed this effect of seed-feeding insects and animals on the plant species in tropical rain forests. I think that his conclusion can be extended to any type of herbivore with strong host preferences. Typically, pioneer communities of plants tend to be composed of a few species at a high density, whereas climax communities have many species at a low density. With plants, no less than with humans, 'possession tends to be nine parts of the law'; hence, having obtained a root hold in a piece of ground, they are not easily displaced by another species. In large part, insects are the 'tenth part of the law' and have the effect of helping plant succession and preventing one species from monopolizing an ecological region. Hodson (1941) reported that outbreaks of the forest tent caterpillar (*Malacosoma disstria* Hueb.) were most pronounced where there were solid stands of its hosts, such as aspen which is a pioneer species. Defoliation for four or five consecutive years produced 20–80 per cent mortality but in some cases he considered this a beneficial natural thinning as it released

the conifers, which were the much more valuable climax species. Similarly, Fox (1948) showed that wireworms in Nova Scotia opened up stands of grass to allow various weeds to flourish. Presumably, this was a step towards the climax forest community of the region. Insecticide control of the wireworms arrested the process; it resulted in the return of grass to its former dominance.

To conclude: if we exclude the topic of insect pollinators, the main source of information on the effect of insects on the population dynamics of plants is from the biological control of weeds. Assuming that the insect introduced to control a weed can build up a large population, the usual effect has been that a low density and scattered distribution of the weed is produced and maintained. The effect may occur over only part of the ecological range of the weed and may be modified by climate or other ecological factors, in such a way that fluctuations in the weed population are produced. However, the main effect of insects is to produce rather stable plant communities of many species, each at low density.

DISCUSSION

Dr J.P.Dempster: In a study of cinnabar moth in the Brecklands here in Norfolk, we observe violent fluctuations of the moth which lead in turn to fluctuations in plant numbers. On the poor soil there, the plant does not regenerate from the crown as you described, but from root buds. In a year following defoliation, if the summer is wet, we have certainly seen an eight-fold multiplication of the plant as a result of defoliation. This is thus an example where, given the right conditions in terms of soil and climate, the effects of defoliation can be just the reverse of what one is looking for in biological control of weeds.

Dr Harris: Is it possible that you have the virus disease in your population? This disease is not present in our Canadian populations.

Dr J.P.Dempster: We do not have the disease here, either—at least, we have not been able to demonstrate it.

Dr Harris: We do have a microsporidian disease in the population on the west coast. This seems just to hasten the mortality of starving individuals but does not seem to have much effect on the population. My inclination on this west coast is to bring in the fleabeetle *Longitarsus jacobaeae* Wat. to put a stress on the root crown of the plant over winter.

Mr S.R.Bowden: Surely in East Anglia one is dealing with an indigenous cinnabar moth population?

Dr J.P.Dempster: Yes.

Mr R.Bardner: Agricultural entomologists like me often think about crops rather than individual plants. Here the *distribution* of the insects has an immense effect particularly on annual crops, because it affects so much the compensatory growth the crop can make. One aphid per plant is very different from 10,000 aphids on one plant out of 10,000. A lot of pests of annual crops seem to have evolved a system by which they space themselves out—plants which they infest are not attacked by other insects and this enables the pests to make the most use of the plants without killing out a patch of plants.

Dr Harris: Yes, I agree about the importance of distribution. But I do think the situation

suited for biological control of weeds is where the weed forms an almost pure stand over relatively large areas. This is why we have insect problems in crop monoculture. The pure stand is the situation which the insect is 'trying' to break up.

Mr F.D.Bennett: You mentioned the fear that insects damaging aquatic weeds might in fact create more plants and spread the weed. This has in fact been demonstrated with *Eichhornia* attacked by a large noctuid. The other observation I would like to make refers to your illustration of *Hypericum* along a railway before and after weed control; aesthetically, the 'before' picture was much nicer. In St Kitt's in the West Indies we had a similar situation with *Tribulus cistoides* L., introduced accidentally around the airport. A weevil was introduced to control the weed when it spread on to pasture land. The stands of the weed along the airport approaches are now decimated and people are actually complaining.

Mr F.Wilson: I want to refer to three examples of 'accidental' biological control of plants affecting climax vegetation. Two scale insects were accidentally introduced on to Bermuda cedar in Bermuda and this completely or very substantially removed cedar from the islands when in fact it had been claimed that it was not possible to apply biological control.

To take another case, a fungus was accidentally introduced to chestnut in North America and caused an immense mortality of the tree in certain parts of the U.S.A.

Thirdly, there is the very important case in New Zealand of *Leptospermum* which occurred over vast areas, but these were enormously reduced following the accidental introduction of scale insects from Australia. The subsequent appearance of a fungus which attacked the scales in particular areas resulted in the recurrence of *Leptospermum*.

I think these examples of 'accidental' biological control are of particular interest because they illustrate effects on climax vegetation. It seems possible that such vegetation in some instances may be climax vegetation because its natural enemies are adequately controlled by other natural enemies.

Professor G.C.Varley: If I may add another example rather nearer home, the maritime pine which has been dominant, with oak sub-dominant, in the hills between Nice and Marseilles has become infested with *Matsucoccus*. The forest is now reverting to oak as the *Matsucoccus* kills the pine over very large areas.

Dr Harris: I think your example is very interesting because spruce is climax in much of Canada. If the spruce sawfly epidemic had continued, you would have got a mixture with many hardwoods coming in—I'm quite sure of this.

Mr F.Wilson: The important feature of all this is that people tend to think in terms of biological control of weeds applied to herbaceous species. You emphasized this yourself. It does seem to me that the basic elements involved are also to be found in more permanent features of the vegetation.

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